Life in a Central European warm-temperate to subtropical open forest: paleoecology of the rhinocerotids from Ulm-Westtangente (Aquitanian, early Miocene, Germany)

Authors: Manon Hullot[1], Céline Martin[2], Cécile Blondel[3], Gertrud Rößner[1, 4]

1 – Bayerische Staatssammlung für Paläontologie und Geologie, Richard-Wagner Straße, 10 8033 München, Germany

2 – Géosciences Montpellier, Université de Montpellier Bât 22 – Place Eugène Bataillon, 34090, Montpellier, France

3 – PALEVOPRIM Poitiers, Université de Poitiers Bât B35 – TSA 51106, 6 rue Michel Brunet, 86073, Poitiers, France

4 – Department für Geo- und Umweltwissenschaften, Paläontologie & Geobiologie, Ludwig-Maximilians-Universität München, Richard-Wagner-Strasse 10, 80333, Munich, Germany

Abstract

The locality of Ulm-Westtangente yielded the richest vertebrate fauna from the Aquitanian (23.03 to 20.44 Mya; early Miocene) of Germany. Its dating to the Mammal Neogene Zone 2a, a turnover in Cenozoic climate, makes it a crucial source for the understanding of faunal, palaeoecological and palaeoenvironmental specifics of the European Aquitanian. However, if most taxa from Ulm-Westtangente have been studied, very little or nothing has been done on the large herbivores and notably the two rhinocerotids *Mesaceratherium paulhiacense* and *Protaceratherium minutum*. Here, we used a multi-proxy approach to investigate the paleoecology of these two species. The remains of the smaller species *P. minutum* (body mass based on teeth: 442 to 667 kg) are twice as abundant as those of the larger *M. paulhiacense* (1687 to 2576 kg), but both display a similar age structure with around 10 % of juveniles, 20 % of subadults and 70 % of adults. Results from mesowear, microwear, and carbon isotopes indicate different feeding preferences for the two species at Ulm-Westtangente: both were C3 feeders but *M. paulhiacense* had a more abrasive diet and was probably a mixed feeder inhabiting a wider range of habitats. Both species had similar mortality curves revealing four mortality peaks correlated with life events: birth or shortly after (age classes I and II), juvenile diseases (IV), weaning (VI-VII), and sexual maturity (IX-X). They were also similarly affected by hypoplasia,

with about 17 % of teeth bearing at least one defect, but the most affected loci did not always correlate with the events highlighted by the mortality curves. Our study on rhinocerotids also yielded new paleoenvironmental insights, such as the mean annual temperature (19.2 °C), confirming the warm-temperate to subtropical conditions previously inferred.

Keywords: diet, habitat, niche partioning, Freshwater Molasse Germany

Introduction

The early Miocene is a key period in Rhinocerotidae evolution, as it was a time of great diversification and geographical expansion. Indeed, the family experienced a peak of alpha-diversity during late early Miocene with several sympatric species at the single fossil sites (Antoine and Becker, 2013). The early Miocene is also marked by a turnover and a great endemism in rhinoceros species of Western Europe. Despite all these, the paleoecology of rhinocerotids during this important time period has rarely been studied, although it has the potential to unravel niche partioning and ecological shifts associated with climatic conditions (Hullot et al., 2023a, 2023b).

One of the richest fossil mammal localities of the early Miocene (Aquitanian: 23.04 – 20.44 Mya; Raffi et al., 2020) in Europe is Ulm-Westtangente in Germany (Heizmann et al., 1989; Costeur et al., 2012). Ulm-Westtangente is located in the Lower Freshwater Molasse sediments of the Baden-Württemberg Basin in Southwestern Germany, about 5 km North-West of Ulm (590 m above sea level, coordinates: 48.418321 N, 9.933701 E – Gauss Kruger coordinates in original publication of Heizmann et al., 1989: r 35 69 188, h 53 64 925). It has been dated to the early Miocene by correlation with the Mammal Neogene-Zone 2a (MN2a; Bruijn et al., 1992; Steininger, 1999), an interval with relatively warm and stable climatic conditions following the cold start of the Miocene (MN1) due to the Mi-1 glaciation event (Zachos et al., 2001; Westerhold et al., 2020). A single 35 cm-thick layer has yielded more than 60 mammal species, making it the richest vertebrate fauna from the early Miocene ever found in Germany (Heizmann et al., 1989; Costeur et al., 2012). Among the numerous fossil remains excavated (~ 6000 from large mammals, > 6000 from small mammals and > 1000 from other vertebrates; Heizmann et al., 1989), abundant material has been attributed to two species of rhinocerotids: the small tapir-sized *Protaceratherium minutum* and the medium to large sized

Mesaceratherium paulhiacense. However, if several taxa have been well studied at the locality rodents and lagomorphs: Werner, 1994; suids: Hellmund, 1991; carnivores: Heizmann and Morlo, 1994; Peigné and Heizmann, 2003; lizards: Klembara et al., 2017; all fauna: Heizmann et al., 1989; Costeur et al., 2012), it is not the case of large herbivores, and notably the rhinocerotids.

The locality of Ulm-Westtangente thus provides a unique opportunity to investigate rhinocerotids paleoecology at a key step of their evolutionary history. Here, we used a multi-proxy approach including diet proxies at different time scales ($\delta^{13}C$, first years of life; dental microwear, last days to months; and mesowear, general lifetime), habitat proxies ($\delta^{18}O$ and $\delta^{13}C$: temperature, precipitation, habitat openness), life history proxies (enamel hypoplasia, body mass prediction, mortality curves: metabolic and environmental stresses, age structure, vulnerability periods). The combination of independent methods is intended to yield more robust results by compensating weaknesses of individual approaches, with the potential to shed light on new aspects and refine complex patterns. This will allow us to discuss niche partitioning, to propose paleoenvironmental interpretations and to provide new data for the understanding of the faunal turnover around the Oligocene-Miocene transition and the early diversification of the Rhinocerotidae in Europe.

Abbreviations

Capital letters are used for the upper teeth (D: deciduous molar; P: premolar; M: molar), while lower case letters indicate lower teeth (d, p, m). Institutional abbreviations: SMNS – Staatliches Museum für Naturkunde Stuttgart, Germany.

Materials and methods

The material studied is curated at the SMNS. It is composed of a total of 492 teeth: 337 of *Protaceratherium minutum* (137 isolated teeth, 200 from four skulls, two maxillae, 18 hemi-mandibles and mandibles, and 13 sets of associated isolated teeth) and 155 of *Mesaceratherium paulhiacense* (73 isolated teeth, 82 from two maxillae, seven hemi-mandibles and mandibles, and nine sets of associated isolated teeth; see Supplementary 1). The number of teeth studied with each method depended on the associated constraints (e.g., only averaged-worn upper molars with cusps preserved on ectoloph profile for mesowear)

and is detailed thereafter (Table 1). Regarding isotopic content, the sample is very limited, as we focused on identifiable fragments (species and locus) as the method is destructive.

Table 1: Number of specimens studied by method and species of rhinocerotids from Ulm-Westtangente

		Protaceratherium minutum	*Mesaceratherium paulhiacense*
Mesowear		16	12
Microwear			
	Grinding	12	12
	Shearing	3	5
Enamel hypoplasia		317	149
Body mass		54	24
Stable isotopy ($\delta^{18}O$, $\delta^{13}C$)		3	5
Mortality curves		336	155

Mesowear

Mesowear is the categorization of gross dental wear into herbivore diet categories. Traditionally, it is based on scoring cusp shape and occlusal relief on upper molars (Fortelius and Solounias, 2000). Here, we used the microwear ruler developed by Mihlbachler et al. (2011) in horses (close relatives of rhinoceros), that gives scores from 0 (high sharp) to 6 (low blunt; see Supplementary 2 Fig 1). With this method browsers have low scores (attrition – tooth-tooth-contact - dominated) and grazers high ones (abrasion – tooth-diet-contact - dominated), while mixed-feeders have intermediate values. Contrary to most studies on mesowear, we consistently scored the paracone and not the sharpest buccal cusp (metacone or paracone), as important differences are noted between these two cusps in rhinoceros (Taylor et al., 2013; Hullot et al., 2021). Eventually, as mesowear score can be affected both by age and hypsodonty (Fortelius and Solounias, 2000),

we only scored upper molars with an average wear (wear stages 4 to 7 from Hillman-Smith et al., 1986) and we compared the hypsodonty index (height of m3 divided by its width; Janis, 1988) of both species.

Dental Microwear Texture Analyses (DMTA)

Dental microwear texture analyses (DMTA) study dietary preferences at a short term scale (day to months; Hoffman et al., 2015). This technique examines tooth surface and identifies wear patterns associated with the different diet categories. In this study, we followed a protocol adapted from Scott et al. (2005) using scale-sensitive fractal analyses. We selected well-preserved molars (upper and lower, left and right) and sampled wear facets from both phases of the mastication (grinding and shearing) on the same enamel band near the protocone, protoconid or hypoconid (see Supplemetary 2 Fig 2). Facets were cleaned twice using a cotton swab soaked in acetone to remove dirt, grit and glue. Then two silicone molds (Coltene Whaledent PRESIDENT The Original Regular Body, ref. 60019939) were made. The second one was used for the analyses described hereafter.

The facet was cut out of the mold, put flat under a Leica Map DCM8 profilometer (TRIDENT, PALEVOPRIM Poitiers) and scanned using white light confocal technology with a 100× objective (Leica Microsystems; Numerical aperture: 0.90; working distance: 0.9 mm). Using LeicaMap (v.8.2; Leica Microsystems), we pre-treated the obtained scans (.plu files) as follows: inversion of the surface (as they come from negative replica), replacement of the missing points (i.e, non-measured, less than 1%) by the mean of the neighboring points, removal of aberrant peaks (automatic operators including a morphological filter see supplementary Information in Merceron et al., (2016b), leveling of the surface, removal of form (polynomial of degree 8) and selection of a 200 × 200 µm area (1551 × 1551 pixels) saved as a digital elevation model (.sur) to be used for DMTA. We conducted scale-sensitive fractal analyses on the selected surfaces (200 × 200 µm; see Supplementary 3) using MountainsMaps® (v.8.2). Our study will focus on the following texture variables, described in detail in Scott et al. (2006):

- anisotropy or exact proportion of length-scale anisotropy of relief (epLsar) is a measure of the orientation concentration of surface roughness; in MountainsMaps®, this parameter has been corrected (NewepLsar), as there was an error in the code of Toothfrax (software previously used for DMTA but not supported anymore; Calandra et al., 2022);
- complexity or area-scale fractal complexity (Asfc) assesses the roughness at a given scale;

- heterogeneity of the complexity (Hasfc) gives information of the variation of complexity at a given scale (here 3 × 3 and 9 × 9) within the studied 200 × 200 µm zone.

Body mass estimations

Body mass is linked to many physiological and ecological parameters (e.g., diet, metabolism, heat evacuation; Peters, 1983; Owen-Smith, 1988; Clauss et al., 2003). Many studies have established equations to estimate fossil body mass based on various dental and limb bone proxies (see the review of Hopkins, 2018). Here, we chose to use several dental proxies, as we studied teeth for all other methods and as they are abundant and well preserved in the fossil record. Each dental proxy and its associated established equation is listed in Table 2 alongside with the corresponding references.

Table 2: List of the dental proxies and the associated equations used to estimate body mass in this study

Measurements are in mm for all equations and give body mass in kg for Janis (1990) and in g otherwise.

Locus	Equation	Reference
m1		
	ln(m) = 1.5133 * ln(m1 length * width) + 3.6515	Legendre (1989)
	log(m) = 3.26 * log(m1 length/10) + 1.337	Janis (1990)
m2		
	log(m) = 3.2 * log(m2 length/10) + 1.13	Janis (1990)
	log(m) = 3.07 * log(m2 length) + 1.07	Damuth (1990)
M1		
	ln(m) = 3.19 * ln(M1 length) + 2.1	Fortelius and Kappelman (1993)
M2		
	log(m) = 3.18 * log(M2 length/10) + 1.091	Janis (1990)
	log(m) = 3.03 * log(M2 length) + 1.06	Damuth (1990)
	ln(m) = 3.09 * ln(M2 length) + 2.14	Fortelius & Kappelman, 1993

Hypoplasia

Hypoplasia is a permanent and sensitive defect of the enamel that has been correlated with stresses, notably environmental (Kierdorf et al., 2012; Skinner and Pruetz, 2012; Upex and Dobney, 2012). It is however non specific and can take several forms, the etiology of which is not well understood (Small and Murray, 1978). In the literature, no standard protocol, nor threshold between normal and pathological enamel are available, so we followed a classical approach that consists in recording and categorizing the defects following the *Fédération Dentaire Internationale* (1982). This index recognizes three main types of defects: linear (line around the crown), pitted (restricted rounded defect) and aplasia (extended zone missing enamel; see Supplemetary 2 Fig 3). In parallel, we recorded several parameters (distance to enamel-dentin junction, width if applicable, localization on the tooth, severity). We studied all available identified cheek teeth, both deciduous and permanent, with the exception of very worn (wear stage 9 and 10 defined by Hillman-Smith et al., 1986) or damaged teeth (i.e., with limited to no enamel preserved) to limit the risk of false negatives. This resulted in the exclusion of 26 teeth (20 of *P. minutum* and six of *M. paulhiacense*) and left 466 teeth to study.

Mortality curves and age structure

Mortality curves are graphs indicating the number of individuals from a sample dying at each age category. They are often used to study taphonomy (attritional causes) and to infer population structure in ancient communities (Fernandez and Legendre, 2003; Bacon et al., 2018). Here, we used a protocol specifically designed for rhinocerotids detailed in Hullot and Antoine (2020). Age estimation is based on the correspondence between wear stages (1-10) and age classes (0-XVI) defined by Hillman-Smith et al. (1986) for each tooth locus. Mortality curves can then be established by following the steps hereunder:

- each tooth is considered individually and has a weight of 1;
- estimation of the wear stage (1 to 10) for each tooth;
- proposal of one or several age classes corresponding to the wear observed for the locus concerned;
- equal weight given to each age class (1 if one, ½ if two...);
- for associated teeth, grouping of all teeth to propose a single class or combination of weighted classes;
- construction of mortality curves from the weighted classes.

Based on the individual ages estimated following the steps above, we calculated the age structure of our sample. Ontogenetic stages are defined as follows, based on the correlations from Hullot and Antoine (2020). Juveniles (birth to weaning) include age classes from I to V, corresponding to 1.5 months to 3 years in the extant white rhinoceros and ending with the eruption of the first permanent teeth (m1/M1). Subadults (weaning to sexual maturity) correspond to age classes VI to VIII (i.e., 3 to 7 years), ending with the eruption of the last permanent teeth (m3/M3). Adults (sexual maturity to death) correlates with age classes IX to XVI (i.e., 7 to 40 years), after the eruption of the last permanent teeth (m3/M3).

Minimum number of individuals

The minimum number of individuals (MNI) is the smallest number of individuals of the same species that can be identified from a fossil assemblage. It is determined by the count of the most abundant anatomical element from the same side (e.g., left femurs, right M3s). Here, estimations also took into account the incompatibility groups based on pattern of dental eruption defined by Hullot and Antoine (2020): for instance milk teeth are never associated in a functioning tooth row with fourth premolars (group b) nor third molars (group a).

Isotopic analyses

Stables isotopes are often used in paleontology as they allow for dietary and environmental insights into terrestrial and aquatic ecosystems (Cerling et al., 1997; Clementz, 2012). Here, we studied $\delta^{13}C$ – linked to the feeding behavior (C3-C4 plants) and to the habitat openness – and $\delta^{18}O$ – that depends on temperature and precipitation – of the carbonates from dental enamel of both rhinocerotid species from Ulm-Westtangente. The $\delta^{18}O$ of rhinoceros enamel is especially interesting for climatic/environmental reconstructions as the animals were abundant and large sized, with a drinking behavior likely resulting in a $\delta^{18}O$ accurately recording the meteoritic precipitation (Clauss et al., 2005; Levin et al., 2006; Martin et al., 2008; Zanazzi et al., 2022).

After mechanical cleaning of a small zone, samples were taken on identified tooth fragments (taxon and locus), preferably from third molars to avoid pre-weaning or weaning signal, using a Dremmel© equipped with a diamond tip. Between 500 and 1000 µg were then used for the analyses. Organic matter was removed following standard procedures (Cerling et al., 1997) and the samples were then acidified with

phosphoric acid (103 %), producing carbon monoxide to be analyzed for isotopic content using a Micromass Optima Isotope Ratio Mass Spectrometer (Géosciences Montpellier). Results are expressed as ratio (‰) to the Vienna-Pee Dee Belemnite standard as follows:

$\delta = 1000 \times (\frac{R_{sample}}{R_{standard}} - 1)$ where R_{sample} refers to the ratio of $\frac{^{13}C}{^{12}C}$ and $\frac{^{18}O}{^{16}O}$ of the sample and $R_{standard}$ to the Vienna-Pee Dee Belemnite standard. The within-run precision (± 1 σ) of these analyses as determined by the replicate analyses of NBS 18 and AIEA-603 was less than ± 0.2 ‰ for $\delta^{13}C$ and ± 0.3 ‰ for $\delta^{18}O$ (n = 5-6 respectively).

The $\delta^{13}C_{diet}$ can be traced back from $\delta^{13}C_{C,\ enamel}$ taking into account the body mass and the digestive system (Tejada-Lara et al., 2018) as detailed below:

$$\varepsilon^*_{diet-bioapatite} = e^{2.42 + 0.032 \times \ln(body\ mass)}$$

$$\delta^{13}C_{diet} = 1000 \times \frac{\delta^{13}C_{C,enamel} - \varepsilon^*_{diet-bioapatite}}{\varepsilon^*_{diet-bioapatite} + 1000}$$

The $\delta^{13}C_{diet}$ can in turn provide the mean annual precipitation (MAP) with the equation from Kohn (2010):

$$\mathrm{MAP} = 10^{\left(\frac{-\delta^{13}C_{diet} + 10.29 + 0.0124 \times |\mathrm{latitude}| - 1.9 \times 10^{-4} \times \mathrm{altitude}}{5.61}\right)} - 300$$

The $\delta^{18}O_{C(V\text{-}PDB)}$ was converted into $\delta^{18}O_{C(V\text{-}SMOW)}$ using the equation from Coplen et al. (1983):

$$\delta^{18}O_{V-SMOW} = 1.03091 \times \delta^{18}O_{V-PDB} + 30.91$$

This was used to calculate the $\delta^{18}O_{precipitation}$ and the mean annual temperature (MAT) detailed as follows. Tütken et al. (2006) provided an equation to estimate the $\delta^{18}O_{precipitation}$ based on the $\delta^{18}O_{PO4}$ of modern rhinoceros. This equation can however be expressed in relation to the $\delta^{18}O_{CO3}$ that we studied here:

$$\delta^{18}O_{precipitation} = (0.77 \pm 0.14) \times \delta^{18}O_{C,enamel} - (25.41 \pm 3.75)$$

Eventually, mean annual temperature (MAT; Tütken et al., 2006) can be calculated using the $\delta^{18}O_{precipitation}$ obtained with the equation above.

$$\mathrm{MAT} = \frac{\delta^{18}O_{precipitation} + 14.178}{0.442}$$

Statistics and Figures

All statistics were conducted in R (R Core Team, 2021: v. 4.1.2) equipped with the package tidyr (Wickham and Henry, 2020), MASS (Ripley et al., 2013) and mvnormtest (Jarek, 2012). Following the recent statement of the American Statistical Association (ASA) on p-values (Wasserstein and Lazar, 2016), we favored giving exact values and we tried to be critical regarding the classical thresholds of “statistical significativity”. Figures were done using R packages ggplot2 (Wickham, 2016), cowplot (Wilke, 2020), as well as Inkscape (v. 1.0.1).

Results

Structure of the rhinocerotid sample from Ulm-Westtangente

There are twice as many teeth attributed to *Protaceratherium minutum* (337) than to *Mesaceratherium paulhiacense* (155) at Ulm-Westtangente. The minimum number of individuals (MNI), based on dental remains, is 17 for *P. minutum* (number of left m1) and 10 for *M. paulhiacense* (number of left p3). When dental eruption incompatibility groups are considered, the MNIs are 24 (group b: fourth premolars and milk teeth) and 15 (group d: third milk molars and third premolars) respectively.

Before correction for the duration of the age classes, we observed a single peak centered around age class IX (Figure 1A-B) for both species, although more spread out in *M. paulhiacense* (IX to XII). In the corrected mortality curves (i.e., number at each age class divided by the duration of the age class), similar tendencies were observed for both species (two-sided Kolmogorov-Smirnov test: D = 0.375, p-value = 0.2145), but with a smaller amplitude for the less abundant *M. paulhiacense*. The histograms of both species revealed four distinct peaks, around age classes I-II, IV, VI-VII, and IX (Figure 1C-D).

The age structure of our rhinocerotid sample from Ulm-Westtangente is composed by 10.8 % of all teeth (species merged) belonged to juveniles, 20.2 % to subadults and 69 % to adults. The proportions were similar between both species (Chi2: X-squared = 0.32999, df = 2, p-value = 0.8479), with 10.5 % of juveniles, 18.3 % of subadults and 71.2 % of adults for *M. paulhiacense*, and 11 % of juveniles, 21.2 % of subadults and 67.8 % of adults for *P. minutum* (see details in Supplementary 1).

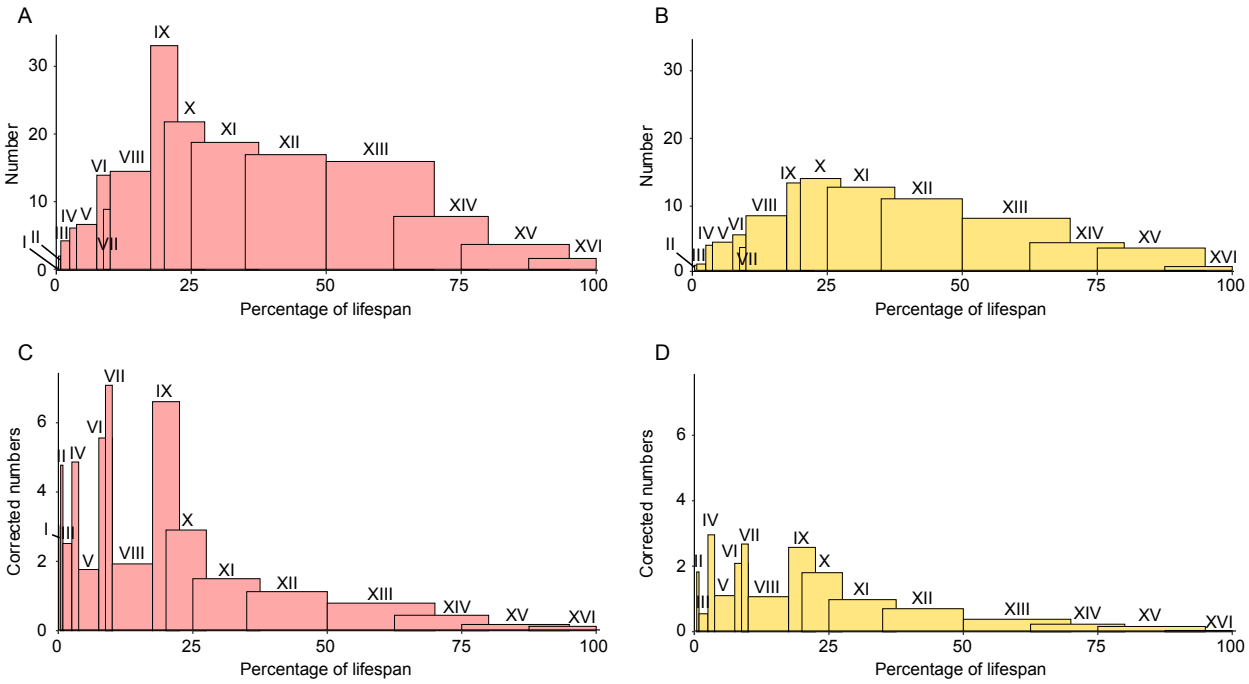

Figure 1: Mortality curves of both rhinocerotid species from Ulm-Westtangente

Number of specimens per age class by species: A – *Protaceratherium minutum*, and B – *Mesaceratherium paulhiacense*

Correction for age class duration (number of specimens divided by the duration of the age class) by species: C – *Protaceratherium minutum*, and D – *Mesaceratherium paulhiacense*

Classes expressed as percentage of lifespan instead of age to limit actualism

Colour code: pink – *Protaceratherium minutum*, yellow – *Mesaceratherium paulhiacense*

Enamel hypoplasia

At Ulm-Westtangente, a total of 79 teeth out of the 466 studied for hypoplasia (16.95 %) bear at least one hypoplastic defect. There are however frequency discrepancies depending on species and tooth loci (Figure 2). Both rhinocerotid species have similar overall hypoplasia prevalences (Kruskal-Wallis test: chi-squared = 0.044163, df = 1, p-value = 0.8336) with 16.7 % (53/317) for *P. minutum* and 17.4 % (26/149) for *M. paulhiacense*. Regarding tooth loci, when both species are merged, four are not affected (only milk molars), 14 have a prevalence of hypoplasia above 10 % and seven above 20 % (Table 3). In general, milk teeth are relatively spared (11.7 to 20 % for D1, D2 and d3) or even not affected (0 % of d1, d2, d4, and D4), with the notable exception of D3 for both species (species merged: 3/5, 40 %), although the sample is very limited (Table 3).

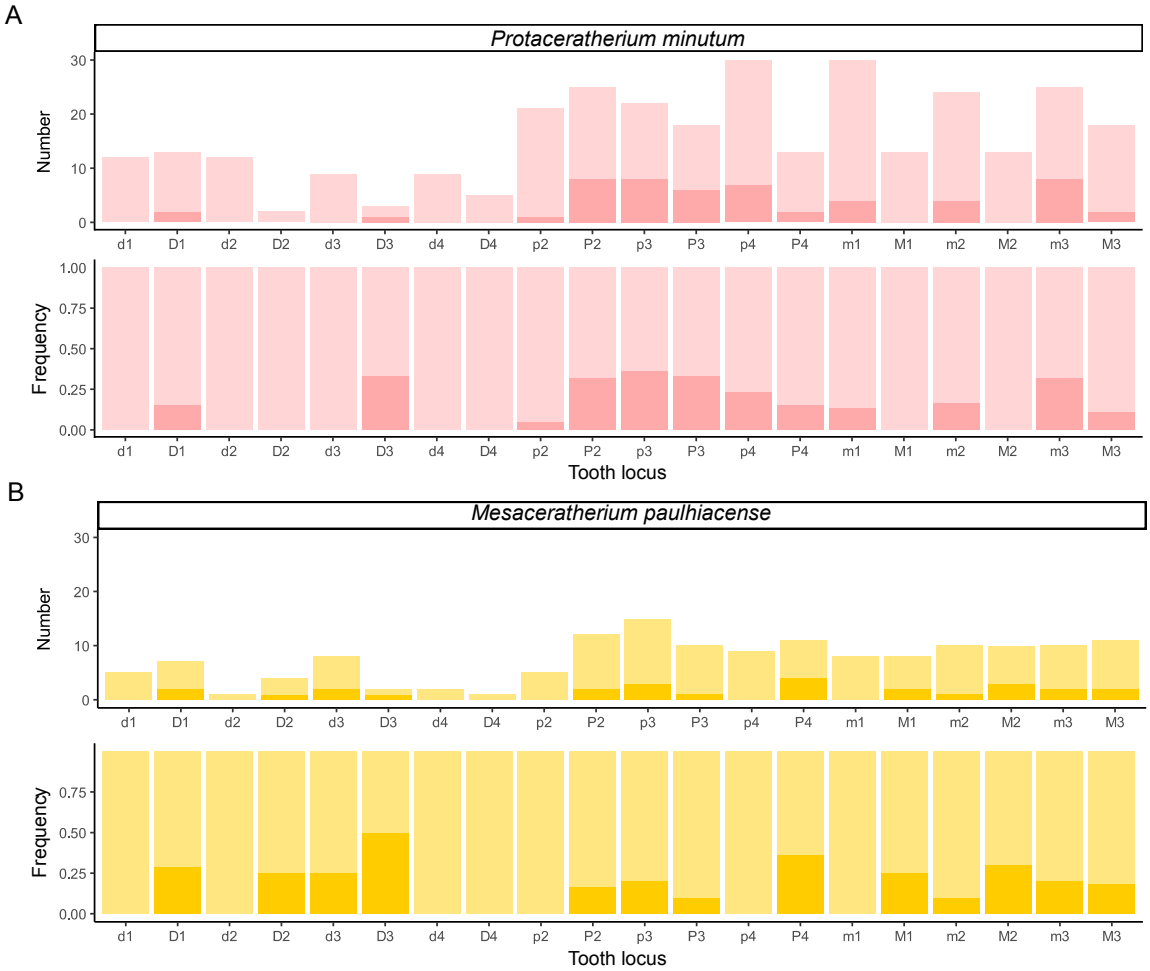

Figure 2: Number and frequency of hypoplasia by locus and species among the rhinocerotids from Ulm-Westtangente

Light colors for unaffected and dark for hypoplastic teeth

A – Number and frequency of hypoplastic teeth vs. unaffected ones for *Protaceratherium minutum*

B - Number and frequency of hypoplastic teeth vs. unaffected ones for *Mesaceratherium paulhiacense*

Table 3: Hypoplasia prevalence by locus (both species merged) at Ulm-Westtangente

Locus	d1	D1	d2	D2	d3	D3	d4	D4	p2	P2	p3	P3	p4	P4	m1	M1	m2	M2	m3	M3
Unaffected	17	16	13	5	15	3	11	6	25	27	26	21	32	18	34	19	29	20	25	25
Affected	0	4	0	1	2	2	0	0	1	10	11	7	7	6	4	2	5	3	10	4
Frequency	0	20	0	16.67	11.76	40	0	0	3.85	27.03	29.73	25	17.95	25	10.53	9.52	14.71	13.04	28.57	13.79

The pattern of loci affected by hypoplasia was however different by species. For *P. minutum*, the most affected teeth were p3 (8/22; 36.4 %), D3 (1/3; 33.3 %), P3 (6/18; 33.3 %), P2 and m3 (each 8/25; 32 %),

while d1, d2, D2, d3, d4, D4, M1, and M2 were never hypoplastic (Figure 2). On the other hand, in *M. paulhiacense* the most affected teeth were D3 (1/2; 50 %), P4 (4/11; 36.4 %), M2 (3/10; 30 %), D1 (2/7; 28.6 %), D2 (1/4; 25 %), d3 (2/8; 25 %) and M1 (2/8; 25 %), while d1, d2, d4, D4, p2, p4, and m1 were never hypoplastic (Figure 2).

Body mass

Both species exhibit obvious differences in size, which is reflected in their body mass estimates, as detailed in Table 4. Mean estimates range from 438 to 685 kg for *P. minutum* and from 1389 to 2327 kg for *M. paulhiacense*, depending on the dental proxy and the equation used.

Table 4: Body mass estimates (in kg) of the rhinocerotids from Ulm-Westtangente based on dental proxies

The number of teeth (n; only one per specimen if both were available) and the mean are shown for each proxy and species. Minimum and maximum estimates are indicated in bold for each species.

		m1		**m2**		**M1**	**M2**		
		Legendre, 1989	Janis, 1990	Janis, 1990	Damuth, 1990	Fortelius and Kappelman, 1993	Janis, 1990	Damuth, 1990	Fortelius and Kappelman, 1993
Protaceratherium minutum									
	n	19	19	16	16	10	9	9	9
	mean	508.93	**685.34**	496.03	**438.11**	474.28	644.10	532.53	487.95
Mesaceratherium paulhiacense									
	n	4	4	7	7	6	7	7	7
	mean	**1389.20**	2043.93	2022.79	1687.06	1935.42	**2327.43**	1811.66	1700.52

Dietary preferences and habitat

Only a few unworn m3 were available to calculate the hypsodonty index (n = 5 for *P. minutum* and n = 3 for *M. paulhiacense*), but both species had relatively similar values (Kruskal-Wallis chi-squared = 1.0889, df = 1, p-value = 0.2967). However, according to the thresholds established by Janis (1988), *P. minutum* classifies as brachyodont (mean hypsodonty index of 1.31), while *M. paulhiacense* is mesodont (mean hypsodonty index of 1.55).

The mesowear scores were contrasted between the two species samples (Table 5; Kruskal-Wallis test: chi-squared = 5.2828, df = 1, p-value = 0.02154). *Protaceratherium minutum* (n = 16) had a mean ruler score of 1.75, with values ranging from 0 (only one tooth) to 3 (only one tooth). On the other hand, *Mesaceratherium paulhiacense* (n = 12) had a higher mean ruler score of 2.25 with values ranging from 1 (only two teeth) to 4 (five teeth). This suggests a more abrasive diet for *M. paulhiacense* consistent with a slightly higher hypsodonty index (mesodont: 1.55, n = 3).

Table 5: Dental wear signatures of the rhinocerotids from Ulm-Westtangente

When several teeth per specimen were available, only one tooth per specimen was studied, preferentially second molars. Gr: grinding facet, Sh: shearing facet, sd: standard deviation

		Protaceratherium minutum			***Mesaceratherium paulhiacense***		
		n	**mean**	**sd**	**n**	**mean**	**sd**
Mesowear		16	1.75	0.68	12	2.25	0.97
Microwear		Gr: 12 Sh: 3			Gr: 12 Sh: 5		
	NewepLsar (*10^{-2})		Gr: 1.69 Sh: 1.91	Gr: 0.17 Sh: 0.38		Gr: 1.69 Sh: 1.87	Gr: 0.12 Sh: 0.19
	Asfc		Gr: 1.72 Sh: 0.62	Gr: 0.99 Sh: 0.16		Gr: 1.27 Sh: 0.77	Gr: 0.71 Sh: 0.22
	Hasfc9		Gr: 0.45 Sh: 0.41	Gr: 0.58 Sh: 0.11		Gr: 0.24 Sh: 0.35	Gr: 0.07 Sh: 0.16
	Hasfc81		Gr: 0.76 Sh: 0.52	Gr: 0.83 Sh: 0.14		Gr: 0.40 Sh: 0.58	Gr: 0.10 Sh: 0.25

The dental microwear texture analyses (DMTA) revealed very contrasted results between grinding and shearing facets (MANOVA: p-value = 0.001), but only for NewepLsar (ANOVA, p-value = 0.02) and Asfc (ANOVA, p-value = 0.004). Regarding species, DMT signatures were relatively similar (Table 5; MANOVA: p-value = 0.69), although some differences might be worth noting. The mean Asfc was lower for the grinding facet of *M. paulhiacense* than that of *P. minutum* (1.27 vs. 1.72), suggesting the processing of slightly softer food items for *M. paulhiacense*. Mean values of HAsfc9 and HAsfc81 were about twice as high for the grinding facet of *P. minutum* (0.45 and 0.76) than *M. paulhiacense* (0.24 and 0.40), but relatively similar for the shearing facet of both species (HAsfc9: 035-0.40; HAsfc81: 0.52-0.58). This indicates a greater diversity of items consumed requiring grinding in *P. minutum*.

The isotopic content of the enamel cabonates for our rhinocerotid sample (n = 8) ranged between -12.76 and -7.47 ‰ for $\delta^{13}C_{C,enamel}$ and -6.04 and -4.78 for $\delta^{18}O_{C,enamel}$. Regarding $\delta^{18}O_{C,\ enamel}$, both rhinocerotids had similar means (Wilcoxon test; W = 6, p-value = 0.7857) with -5.1 ± 0.3 ‰ Vienna Pee Dee Belemnite (VPDB) for *P. minutum* and -5.4 ± 0.4 ‰ VPDB for *M. paulhiacense*, suggesting similar drinking water sources. The mean $\delta^{18}O_{C,\ enamel}$ was however a little lower for *M. paulhiacense*, but this could be due to an outlier for this species (Figure 3A; mean without outlier -5.2 ± 0.1 ‰ VPDB). The $\delta^{18}O_{precipitation}$ (not shown in the graphs) had a mean of -5.7 ± 0.2 ‰ (both species merged, outlier removed), which is significantly higher than today's values that are around -9.3 ‰ (today's value for Ulm, Germany calculated with the Online Isotopes in Precipitation Calculator: https://wateriso.utah.edu/waterisotopes/pages/data_access/oipc.html). The value obtained from the rhinocerotid specimens suggests a mean annual temperature (MAT) of 19.2°C.

Clear differences were observed between both species for $\delta^{13}C_{C,enamel}$ (Wilcoxon test; W = 0, p-value = 0.03571) although they stay in the range of C3 diet and habitat (Figure 3): *P. minutum* had higher values (n = 3, mean = -8.1 ± 0.5 ‰) compared to that of *M. paulhiacense* (n = 5, mean = -10.6 ± 1.5 ‰). Without the outlier (*M. paulhiacense*, mean = 10.1 ± 1 ‰), the difference between the two species for $\delta^{13}C_{C,enamel}$ is less marked (Wilcoxon test; W = 0, p-value = 0.05714), but still suggests different ecologies (diet and/or habitat). The values of $\delta^{13}C_{C,enamel}$ in our sample yielded negative mean annual precipitation (MAP), except for the outlier (MAP = 384 mm/year) and two specimens of *M. paulhiacense* for which the MAP was still very low (< 40 mm/year).

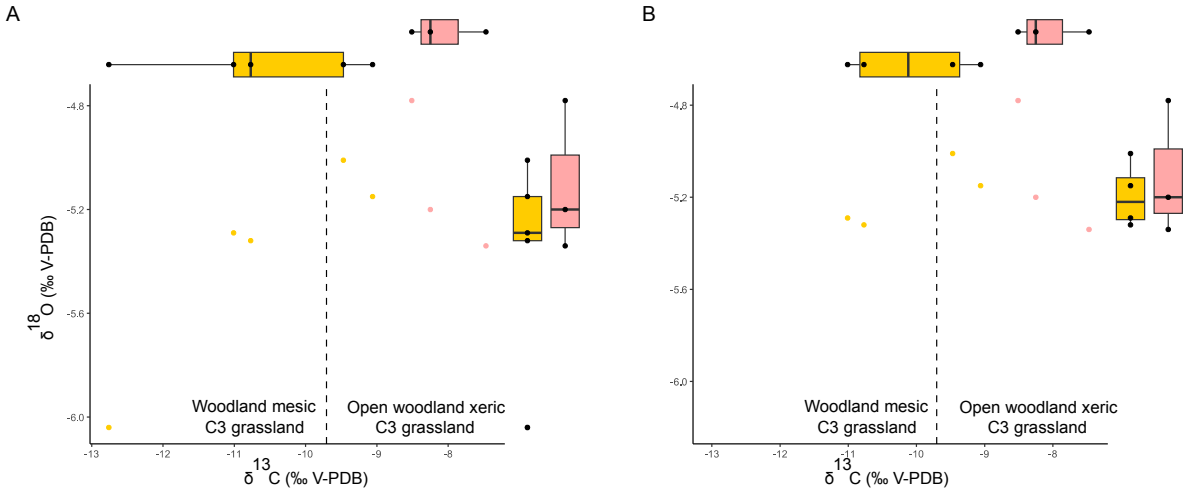

Figure 3: Isotopic composition of the carbonates in the enamel of the two rhinocerotids from Ulm-Westtangente

A- Dotplot of $\delta^{18}O_{C,enamel}$ against $\delta^{13}C_{C,enamel}$ with associated boxplots

B- Same graph without the outlier of *Mesaceratherium paulhiacense*

One specimen of *M, paulhiacense* appeared as an outlier for $\delta^{18}O_{C,enamel}$ (outside whiskers range) and was removed as we suspected a weaning signal

Color code: pink- *Protaceratherium minutum* and yellow- *Mesaceratherium paulhiacense*

Threshold based on the results of Zanazzi et al. (2022) in *Stephanorhinus*.

Discussion

Body mass of the rhinocerotids from Ulm-Westtangente

In extant rhinoceros, one of the most accurate dental proxy appears to be the length of M2 with the equation of Damuth (1990; MH pers. obs.), which here gives means of 532.5 kg for *P. minutum* and 1811.7 kg for *M. paulhiacense* (Table 4). Such a body mass for *P. minutum*, around 500 kg, is consistent with a previous estimation based on the astragalus (Becker, 2003). In their study on Ulm-Westtangente, Costeur et al. (2012) used the occlusal surface of m1 as a proxy for body mass (Legendre, 1989). They found higher means than our study using the same proxy for both species (590 vs. 509 kg and 1752 vs. 1389 kg respectively). Such discrepancies might result from an inter-observer bias, the inclusion of misidentified teeth (e.g., m2 instead of m1), a restricted data set in their study (sampling bias), or the inclusion of worn teeth in

our study (rhinoceros m1 tend to shorten with wear; Antoine pers. comm., MH pers. obs.). In any case, the rhinocerotids are the biggest species found at Ulm-Westtangente (Costeur et al., 2012), with only *M. paulhiacense* exceeding 1000 kg, the threshold for megaherbivores following Owen-Smith (1988). Such a result is not really surprising, as European faunas did not show a high diversity of megaherbivores before the late Early Miocene (Proboscidean Datum Event; Costeur et al., 2012).

Age structure, stress vulnerability and mortality of the rhinocerotids from Ulm-Westtangente

The age structure with around 10 % of juveniles, 20 % of subadults and 70 % of adults for both rhinocerotid samples is close to the structure observed in modern *Diceros bicornis* populations (Supplementary 2 Fig 4; Goddard, 1970; Hitchins, 1978). As Ulm-Westtangente provides a relatively time constrained framework (fossil layer only 35 cm thick; Heizmann et al., 1989), the studied sample could closely reflect living populations of both rhinocerotids with very minor preservation or taphonomic bias. The comparison with extant populations of rhinoceros must, however, be careful, as poaching and population management might have biased the observed age structure.

The mortality curves based on rhinocerotid teeth from Ulm-Westtangente (Figure 1) suggested several vulnerability periods, similar in both species. The first peak is noted for classes I and II (0.31 to 0.83 % of lifespan, i.e. 1.5 to 4 months old in extant *Ceratotherium simum*; Hillman-Smith et al., 1986), and corresponds to the period shortly after birth. Birth is known to be a particularly stressful event in the life of an animal (Upex and Dobney, 2012), and has notably been correlated with the presence of a neonatal line in primate deciduous teeth and first molar (Gustafson and Gustafson, 1967; Risnes, 1998), as well as with hypoplasia on fourth milk molars in several ungulates (rhinoceros: Mead, 1999; bison: Niven et al., 2004; sheep: Upex and Dobney, 2012). In our data set d4/D4 were never affected in either species (Figure 2). This finding is not necessarily contradicting, as the animal must survive the stress for the hypoplasia defect to be visible (Guatelli-Steinberg, 2001). Other loci, that also develop around birth, displayed however a higher prevalence of hypoplasia, especially in *M. paulhiacense*. This is notably the case of the first molar (Tafforeau et al., 2007; Upex and Dobney, 2012), which was amongst the most affected loci in *M. paulhiacense* (25 % of M1; Figure 2), or of other milk teeth loci suggesting early life stresses (or even *in utero*; Figure 2).

The second peak is observed at age class IV (2.5 to 3.75 % of lifespan, i.e. 1 to 1.5 years old), which could be a sign of juvenile diseases. Hypoplasia in fossil rhinoceros has previously been linked to juvenile malnutrition or disease causing a fever (Bratlund, 1999), although no specific locus was mentioned. Based on the timing of tooth development in extant rhinoceros, hypoplasia due to juvenile diseases could impact all premolars and molars but m3/M3 (chapter IV, page 131: Hullot, 2021). All these loci are affected in our data set, with a variable prevalence depending on the species, but a direct correlation with juvenile diseases is not straight forward.

The third peak corresponds to age classes VI-VII (7.5 to 10 % of lifespan, i.e. 3 to 4 years old), which are correlated to the period shortly after weaning (Hullot and Antoine, 2020), maybe indicating cow-calf separation. Weaning and cow-calf separation are known to be critical times for many extant mammals, including rhinoceroses. Indeed, at that time, adult size is not yet reached (Owen-Smith, 1988), leading to a higher predation risk (Brain et al., 1999). In parallel, calves might experience food stresses (Mead, 1999) due to their new independence. Interestingly, both events have been associated with hypoplastic defects in primates and pigs (Goodman and Rose, 1990; Dobney and Ervynck, 2000; Guatelli-Steinberg, 2001; Skinner and Pruetz, 2012). In fossil rhinoceroses, Mead (1999) supposed that hypoplasia on the fourth premolars might be associated with cow-calf separation. Here, fourth premolars are mildly to highly affected (15 to 36 %) for both species (Figure 2, Table 3), which could suggest that cow-calf separation was also a stressful event in these fossil species. Moreover, in modern rhinoceroses, second molars develop at a relatively similar timing than that of fourth premolars (Goddard, 1970; Hitchins, 1978; Hillman-Smith et al., 1986). Interestingly, P4 and M2 commonly bear at least one hypoplastic defect in *M. paulhiacense* (Figure 2).

Eventually, a last peak in mortality is observed around classes IX-X (17.5 to 27.5 % of lifespan, i.e. 7 to 11 years old), correlating with sexual maturity (Hullot and Antoine, 2020). In modern rhinoceroses, courtship and mating can be violent, including male fights for dominance, male rejection by the female, female chasing by males or mating wounds (Owen-Smith, 1988; Zecchini, 1998; Dinerstein, 2003), all of which could explain the increase of mortality observed for these age classes. However, potential stresses associated with this last peak were not recorded by enamel hypoplasia, as they occurred post-odontogenetically.

Paleoecology of the rhinocerotids from Ulm-Westtangente

Overall, results from carbon isotopic content, meso- and micro-wear suggest different dietary preferences for the two rhinocerotid species at Ulm-Westtangente. The isotopic signal ($\delta^{13}C_{C,\ enamel}$) of both species falls in the range of C3 feeding (< -8-9 ‰; Stefaniak et al., 2020; Zanazzi et al., 2022) but points towards different habitats and/or dietary preferences. Based on the thresholds proposed by Zanazzi et al. (2022) in *Stephanorhinus*, *M. paulhiacense* appears to have inhabited both open woodland xeric C3 grassland and woodland mesic C3 grassland, whereas *P. minutum* seems restricted to the first one (Figure 3). This last finding is in line with what has been inferred based on morphology, as *Protaceratherium minutum* is described as a cursorial brachyodont species typical of forested, partially open environments (Becker, 2003).

Regarding mesowear, *M. paulhiacense* has a higher mean score (2.25) than *P. minutum* (1.75), pointing towards a more abrasive diet (Table 5). Interestingly, *M. paulhiacense* has a slightly higher hypsodonty index and is also bigger (Table 4), which is often associated to a supposedly higher tolerance to low quality, more fibrous and abrasive diet (Jarman-Bell principle; Clauss et al., 2013; Steuer et al., 2014). The mesowear values observed for *P. minutum* (mostly 1 or 2) are consistent with browsing but also overlap with mixed-feeding, whereas that for *M. paulhiacense* (2, 3 and 4) point towards mixed-feeding or grazing (Rivals et al., 2017). However, a C4-grazing is unlikely based on the isotopic signal (Figure 3), the age and the situation of Ulm-Westtangente (C4 scarce or absent in the early Miocene of Germany; Strömberg, 2011).

Fewer differences were noted in the microwear pattern of both species (Table 5). The DMT is rather consistent with the mesowear, and points towards mixed-feeding in *P. minutum* (high values of Hasfc correlated with diversity in the diet; Scott et al., 2006). For *M. paulhiacense* the low values of Asfc suggest soft browsing, while mesowear scores indicate more abrasion. The consumption of leaves, that are abrasive but soft items, could reconciliate both, although anisotropy is normally high in folivore (Scott, 2012; Hullot et al., 2019). This last observation could however be biased by the previous use of epLsar, which had an error in the code for its extraction (Calandra et al., 2022).

Outlier in the stable isotope dataset: weaning signal?

One tooth of *M. paulhiacense* has significantly lower values for both $\delta^{13}C_{C,enamel}$ and $\delta^{18}O_{C,enamel}$ (Figure 3) than the rest of the sampled teeth and, hence, was considered as an outlier. Interestingly, this is the only premolar of our data set (P4). Such different isotopic contents could be the result of a sampling in the pre-weaning part of the P4, as this tooth is known to partly develop before weaning in several extant rhinoceros species (Goddard, 1970; Hitchins, 1978; Hillman-Smith et al., 1986; Mead, 1999). Indeed, milk has a higher $\delta^{18}O$ than drinking water due to the preferential loss of the light oxygen isotope (^{16}O) through expired and transcutaneous water vapor fluxes (Kohn et al., 1996), as well as a lower $\delta^{13}C$ than plants due to the presence of lipids, which are depleted in ^{13}C relatively to other macronutrients (DeNiro and Epstein, 1977). The carbon depletion might however be relatively limited in the case of rhinoceros, as the milk of living individuals has a very low lipid content (Osthoff et al., 2021).

Associated fauna and paleoenvironment

Besides the two rhinocerotids species, the herbivore assemblage at Ulm-Westtangente includes two other perissodactyl species – a chalicothere (cf. *Metaschizotherium wetzleri*) and a tapir (*Paratapirus intermedius*) – five artiodactyl species and 18 rodent and lagomorph species (Heizmann et al., 1989; Costeur et al., 2012). However, the body mass of all these species is significantly lower than that of the rhinocerotids, with only the chalicothere and the tapir ranging between 100 and 200 kg (Costeur et al., 2012), which limits potential competitive interactions. Unfortunately, no precise data is available on the paleoecology of these species, but schizotheriines are often reconstructed as open woodland dwellers (Heissig, 1999) consuming leaves, fruits and maybe seeds and bark (Schulz et al., 2007; Semprebon et al., 2011), while tapirs prefer forested habitats and are typically folivores (DeSantis and MacFadden, 2007).

Regarding environmental conditions, the MAP could not be reliably inferred from our rhinocerotid sample. Indeed, we obtained negative values for most specimens studied, with only three specimens of *M. paulhiacense*, including the outlier mentioned above, yielding very variable positive values of MAP (between 5.6, 37 and 384.3 mm/year; see Supplementary 1). As our sample is limited (n = 8) and restricted to a single taxon (Rhinocerotidae) this outcome is not surprising, as robust estimates of MAP require averaging over multiple species in a single locality (Kohn, 2010). Moreover, other parameters might result in low to negative

MAP, such as the consumption of C4 or the variation of C3 plant isotope compositions within a single locality (Kohn, 2010), revealing the need of a revision in the way MAP is calculated.

Regarding temperature, the study of Costeur et al., (2012), has taken interest in the whole mammal fauna and proposed a cenogram. This study inferred an environment of a warm-temperate forest with grassland habitats at Ulm-Westtangente, but found quite a low MAT, around 7°C. This MAT is similar to the one proposed for Montaigu-le-Blin (France; reference of MN2a) using the same approach. The authors note that this estimation is surprising, as the Aquitanian conditions are reconstructed as warm-temperate or subtropical (Zachos et al., 2001), and argue that this could be a remnant of the Mi-1 glaciation. Here, we found a MAT of about 19°C based on the oxygen content of the enamel from our rhinocerotid sample. Although several complications exist in calculating absolute MAT from $\delta^{18}O_{precipitation}$ (see details in Zanazzi et al., 2022), this result is more consistent with the warm-temperate forest with grassland habitats inferred on species assemblage and cenograms (Costeur et al., 2012), the presence of ectothermic species (Costeur et al., 2012; Klembara et al., 2017), and with the global climate reconstructed at that time (Zachos et al., 2001; Westerhold et al., 2020).

The medium prevalence of hypoplasia in our sample (~ 17 %) also suggests good environmental conditions, although some seasonality can be suspected. Indeed, m3 is amongst the most affected loci especially for *P. minutum* (Figure 2, Table 3), and hypoplasia on third molars has been associated with environmental stresses such as seasonality (Franz-Odendaal et al., 2003; Skinner and Pruetz, 2012; Upex and Dobney, 2012). Periodic floodings are supposed at Ulm-Westtangente and proposed as attritional causes (Heizmann et al., 1989). Such events might result in increased levels of stress through vegetation damage, habitat loss or displacement and decrease of water quality (e.g., Lake et al., 2006). Besides external stressors, an effect of the diet and/or of phylogeny on stress susceptibility has been hypothesized in Miocene rhinocerotids from other sites (Hullot et al., 2023a, 2023b). Here, both species are closely phylogenetically related (early diverging taxa of Aceratheriinae *sensu lato*; Rhinocerotinae *incertae sedis* in Tissier et al. [2020]) and are similarly affected despite having different inferred diets (Table 5), suggesting that phylogeny might be the main driver.

Conclusion

In this article, we provided paleoecological insights for the two rhinocerotid species from the early Miocene locality of Ulm-Westtangente (Germany). All dietary proxies (mesowear, microwear, $\delta^{13}C$) pointed towards different feeding preferences, with a more generalistic behavior for the bigger species *Mesaceratherium paulhiacense*. As the rhinocerotids were by far the biggest species at Ulm-Westtangente, competitive interactions with other herbivores might have been limited. However, the investigation of ecological preferences of the other species associated, especially the chalicothere cf. *Metaschizotherium wetzleri* and the tapir *Paratapirus intermedius*, would be interesting to clarify resources use. The prevalence of hypoplasia was similar in both species (~ 17 %), suggesting a potential greater influence of phylogeny than diet/ecology in stress susceptibility, we identified specific differences in the loci affected. Vulnerability periods correlating with life events (birth, juvenile diseases, weaning and cow calf separation, seasonality) were identified. Some of these vulnerability periods were also highlighted by the mortality curves. Regarding the paleoenvironment, our rhinocerotid sample confirmed the previous inferences of a warm-temperate forest with grassland patches, and gave a mean annual temperature (MAT) of 19.2°C. Previous results gave a significantly lower MAT (7°C) based on the cenogram, thus the inclusion of isotopic data from other taxa and/or the use of serial sampling might provide a more robust calculation and an insight into a potential seasonality.

Acknowledgments

We are grateful to Dr. Eli Amson the curator for fossil mammals at the SMNS for granting access to and providing inventory numbers for the specimens of Ulm-Westtangente. This study was funded by a post doctoral fellowship of the Alexander von Humboldt Foundation (Germany).

References

Antoine, P.-O., and D. Becker. 2013. A brief review of Agenian rhinocerotids in Western Europe. Swiss Journal of Geosciences 106:135–146.

Bacon, A.-M., P.-O. Antoine, N. T. M. Huong, K. Westaway, N. A. Tuan, P. Duringer, J. Zhao, J.-L. Ponche, S. C. Dung, T. H. Nghia, T. T. Minh, P. T. Son, M. Boyon, N. T. K. Thuy, A. Blin, and F. Demeter. 2018. A

rhinocerotid-dominated megafauna at the MIS6-5 transition: The late Middle Pleistocene Coc Muoi assemblage, Lang Son province, Vietnam. Quaternary Science Reviews 186:123–141.
Becker, D. 2003. Paléoécologie et paléoclimats de la molasse du Jura (oligo-miocène). PhD Thesis, Université de Fribourg, 327 pp.
Brain, C., O. Forge, and P. Erb. 1999. Lion predation on black rhinoceros (*Diceros bicornis*) in Etosha National Park. African Journal of Ecology 37:107–109.
Bratlund, B. 1999. Taubach revisited. Jahrbuch Des Römisch-Germanischen Zentralmuseums Mainz 46:61–174.
Bruijn, H. de, R. Daams, G. Daxner-Höck, V. Fahlbusch, L. Ginsburg, P. Mein, J. Morales, E. Heizmann, D. F. Mayhew, A. J. Van der Meulen, N. Schmidt-Kittler, and M. Telles Autunes. 1992. Report of the RCMNS working group on fossil mammals, Reisensburg 1990. Newsletters on Stratigraphy 26:65–118.
Calandra, I., K. Bob, G. Merceron, F. Blateyron, A. Hildebrandt, E. Schulz-Kornas, A. Souron, and D. E. Winkler. 2022. Surface texture analysis in Toothfrax and MountainsMap® SSFA module: Different software packages, different results? Peer Community Journal 2:article no. e77.
Cerling, T. E., J. M. Harris, S. H. Ambrose, M. G. Leakey, and N. Solounias. 1997. Dietary and environmental reconstruction with stable isotope analyses of herbivore tooth enamel from the Miocene locality of Fort Ternan, Kenya. Journal of Human Evolution 33:635–650.
Clauss, M., P. Steuer, D. W. H. Müller, D. Codron, and J. Hummel. 2013. Herbivory and Body Size: Allometries of Diet Quality and Gastrointestinal Physiology, and Implications for Herbivore Ecology and Dinosaur Gigantism. PLOS ONE 8:e68714.
Clauss, M., R. Frey, B. Kiefer, M. Lechner-Doll, W. Loehlein, C. Polster, G. E. Rössner, and W. J. Streich. 2003. The maximum attainable body size of herbivorous mammals: morphophysiological constraints on foregut, and adaptations of hindgut fermenters. Oecologia 136:14–27.
Clauss, M., C. Polster, E. Kienzle, H. Wiesner, K. Baumgartner, F. von Houwald, W. J. Streich, and E. Dierenfeld. 2005. Energy and mineral nutrition and water intake in the captive Indian rhinoceros (*Rhinoceros unicornis*). Zoo Biology 24:1–14.
Clementz, M. T. 2012. New insight from old bones: stable isotope analysis of fossil mammals. Journal of Mammalogy 93:368–380.
Coplen, T. B., C. Kendall, and J. Hopple. 1983. Comparison of stable isotope reference samples. Nature 302:236–238.
Costeur, L., O. Maridet, S. Peigné, and E. P. Heizmann. 2012. Palaeoecology and palaeoenvironment of the Aquitanian locality Ulm-Westtangente (MN2, Lower Freshwater Molasse, Germany). Swiss Journal of Palaeontology 131:183–199.
Damuth, J. 1990. Problems in estimating body masses of archaic ungulates using dental measurements; pp. 229–254 in J. Damuth and B. J. MacFadden (eds.), Body size in mammalian paleobiology: estimation and biological implications, Cambridge University Press.
DeNiro, M. J., and S. Epstein. 1977. Mechanism of Carbon Isotope Fractionation Associated with Lipid Synthesis. Science 197:261–263.
DeSantis, L. R., and B. MacFadden. 2007. Identifying forested environments in deep time using fossil tapirs: evidence from evolutionary morphology and stable isotopes. Courier-Forschungsinstitut Senckenberg 258:147–157.
Dinerstein, E. 2003. The Return of the Unicorns: The Natural History and Conservation of the Greater One-Horned Rhinoceros. Columbia University Press, 344 pp.
Dobney, K., and A. Ervynck. 2000. Interpreting Developmental Stress in Archaeological Pigs: the Chronology of Linear Enamel Hypoplasia. Journal of Archaeological Science 27:597–607.
Fédération Dentaire Internationale. 1982. An epidemiological index of development defects of dental enamel (DDE index). International Dental Journal 42:411–426.
Fernandez, P., and S. Legendre. 2003. Mortality curves for horses from the Middle Palaeolithic site of Bau de l'Aubesier (Vaucluse, France): methodological, palaeo-ethnological, and palaeo-ecological approaches. Journal of Archaeological Science 30:1577–1598.
Fortelius, M., and J. Kappelman. 1993. The largest land mammal ever imagined. Zoological Journal of the Linnean Society 108:85–101.
Fortelius, M., and N. Solounias. 2000. Functional characterization of ungulate molars using the abrasion-attrition wear gradient: a new method for reconstructing paleodiets. American Museum Novitates 2000:1–36.

Franz-Odendaal, T. A., J. A. Lee-Thorp, and A. Chinsamy. 2003. Insights from stable light isotopes on enamel defects and weaning in Pliocene herbivores. Journal of Biosciences 28:765–773.
Goddard, J. 1970. Age criteria and vital statistics of a black rhinoceros population. African Journal of Ecology 8:105–121.
Goodman, A. H., and J. C. Rose. 1990. Assessment of systemic physiological perturbations from dental enamel hypoplasias and associated histological structures. American Journal of Physical Anthropology 33:59–110.
Guatelli-Steinberg, D. 2001. What can developmental defects of enamel reveal about physiological stress in nonhuman primates? Evolutionary Anthropology 10:138–151.
Gustafson, G., and A. G. Gustafson. 1967. Microanatomy and histochemistry of enamel; pp. 75–134 in Structural and chemical organization of teeth. vol. 2. Academic Press New York.
Heissig, K. 1999. Family Chalicotheriidae; pp. 189–192 in G. E. Rössner and K. Heissig (eds.), The Miocene Land Mammals of Europe. Verlag Dr. Friedrich Pfeil, München, Germany.
Heizmann, E. P., and M. Morlo. 1994. *Amphictis schlosseri* n. sp.-eine neue Carnivoren-Art (Mammalia) aus dem Unter-Miozän von Südwestdeutschland. Stuttgarter Beiträge Zur Naturkunde Serie B 216:1–25.
Heizmann, E. P., G. Bloos, G. Bloos, and R. Böttcher. 1989. Ulm-Westtangente und Ulm-Uniklinik: Zwei neue Wirbeltier-Faunen aus der Unteren Süßwasser-Molasse (Untermiozän) von Ulm (Baden-Württemberg). Stuttgarter Beiträge Zur Naturkunde, Serie B 153:1–14.
Hellmund, M. 1991. Schweineartige (Suina, Artiodactyla, Mammalia) aus oligo-miozänen Fundstellen Deutschlands, der Schweiz und Frankreichs: I. *Hyotherium meissneri* (Suidae) aus dem Untermiozän von Ulm-Westtangente (Baden-Württemberg). Stuttgarter Beiträge Zur Naturkunde Serie B 176:1–69.
Hillman-Smith, A. K. K., N. R. Owen-Smith, J. L. Anderson, A. J. Hall-Martin, and J. P. Selaladi. 1986. Age estimation of the white rhinoceros (*Ceratotherium simum*). Journal of Zoology 210:355–377.
Hitchins, P. M. 1978. Age determination of the black rhinoceros (*Diceros bicornis* Linn.) in Zululand. South African Journal of Wildlife Research 8:71–80.
Hoffman, J. M., D. Fraser, and M. T. Clementz. 2015. Controlled feeding trials with ungulates: a new application of in vivo dental molding to assess the abrasive factors of microwear. The Journal of Experimental Biology 218:1538–1547.
Hopkins, S. S. B. 2018. Estimation of Body Size in Fossil Mammals; pp. 7–22 in D. A. Croft, D. F. Su, and S. W. Simpson (eds.), Methods in Paleoecology: Reconstructing Cenozoic Terrestrial Environments and Ecological Communities, Vertebrate Paleobiology and Paleoanthropology Springer International Publishing, Cham.
Hullot, M. 2021. Analyses texturales des micro-usures et des hypoplasies de l'émail dentaire chez les Rhinocerotidae actuels et fossiles (Mammalia, Perissodactyla) : inférences paléobiologiques et paléoécologiques. PhD thesis, Université Montpellier, 390 pp.
Hullot, M., and P.-O. Antoine. 2020. Mortality curves and population structures of late early Miocene Rhinocerotidae (Mammalia, Perissodactyla) remains from the Béon 1 locality of Montréal-du-Gers, France. Palaeogeography, Palaeoclimatology, Palaeoecology 558:109938.
Hullot, M., G. Merceron, and P.-O. Antoine. 2023a. Spatio-temporal diversity of dietary preferences and stress sensibilities of early and middle Miocene Rhinocerotidae from Eurasia: impact of climate changes. Peer Community Journal 3:article e5.
Hullot, M., P.-O. Antoine, M. Ballatore, and G. Merceron. 2019. Dental microwear textures and dietary preferences of extant rhinoceroses (Perissodactyla, Mammalia). Mammal Research 64:397–409.
Hullot, M., Y. Laurent, G. Merceron, and P.-O. Antoine. 2021. Paleoecology of the Rhinocerotidae (Mammalia, Perissodactyla) from Béon 1, Montréal-du-Gers (late early Miocene, SW France): Insights from dental microwear texture analysis, mesowear, and enamel hypoplasia. Palaeontologia Electronica 24:1–26.
Hullot, M., P.-O. Antoine, N. Spassov, G. D. Koufos, and G. Merceron. 2023b. Late Miocene rhinocerotids from the Balkan-Iranian province: ecological insights from dental microwear textures and enamel hypoplasia. Historical Biology 35:1417–1434.
Janis, C. M. 1988. An estimation of tooth volume and hypsodonty indices in ungulate mammals, and the correlation of these factors with dietary preferences. Memoires Du Museum National d' Histoire Naturelle serie C, 53:367–387.
Janis, C. M. 1990. Correlation of cranial and dental variables with body size in ungulates and macropodoids; pp. 255–300 in J. Damuth and B. J. MacFadden (eds.), Body size in mammalian paleobiology:

estimation and biological implications, Cambridge University Press. Cambridge University Press Cambridge, Cambridge.
Slawomir Jarek (2012). mvnormtest: Normality test for multivariate variables. R package version 0.1-9.
Kierdorf, H., C. Witzel, B. Upex, K. Dobney, and U. Kierdorf. 2012. Enamel hypoplasia in molars of sheep and goats, and its relationship to the pattern of tooth crown growth. Journal of Anatomy 220:484–495.
Klembara, J., M. Hain, and A. Čerňanskỳ. 2017. The first record of anguine lizards (Anguimorpha, Anguidae) from the early Miocene locality Ulm–Westtangente in Germany. Historical Biology 31:1016–1027.
Kohn, M. J. 2010. Carbon isotope compositions of terrestrial C3 plants as indicators of (paleo)ecology and (paleo)climate. Proceedings of the National Academy of Sciences 107:19691–19695.
Kohn, M. J., M. J. Schoeninger, and J. W. Valley. 1996. Herbivore tooth oxygen isotope compositions: Effects of diet and physiology. Geochimica et Cosmochimica Acta 60:3889–3896.
Lake, S., N. Bond, and P. Reich. 2006. Floods Down Rivers: From Damaging to Replenishing Forces; pp. 41–62 in Advances in Ecological Research. Floods in an Arid Continent vol. 39. Academic Press.
Legendre, S. 1989. Les Communautés de Mammifères Du Paléogène (Eocène Supérieur et Oligocène) d'Europe Occidentale : Structures, Milieux et Évolution, Münchner Geowissenschaftliche Abhandlungen. München, Germany, 1–110 pp.
Levin, N. E., T. E. Cerling, B. H. Passey, J. M. Harris, and J. R. Ehleringer. 2006. A stable isotope aridity index for terrestrial environments. Proceedings of the National Academy of Sciences 103:11201–11205.
Martin, C., I. Bentaleb, R. Kaandorp, P. Iacumin, and K. Chatri. 2008. Intra-tooth study of modern rhinoceros enamel $\delta^{18}O$: Is the difference between phosphate and carbonate $\delta^{18}O$ a sound diagenetic test? Palaeogeography, Palaeoclimatology, Palaeoecology 266:183–189.
Mead, A. J. 1999. Enamel hypoplasia in Miocene rhinoceroses (*Teleoceras*) from Nebraska: evidence of severe physiological stress. Journal of Vertebrate Paleontology 19:391–397.
Merceron, G., A. Ramdarshan, C. Blondel, J.-R. Boisserie, N. Brunetiere, A. Francisco, D. Gautier, X. Milhet, A. Novello, and D. Pret. 2016. Untangling the environmental from the dietary: dust does not matter. Proceedings of the Royal Society B: Biological Sciences 283:20161032.
Mihlbachler, M. C., F. Rivals, N. Solounias, and G. M. Semprebon. 2011. Dietary change and evolution of horses in North America. Science 331:1178–1181.
Niven, L. B., C. P. Egeland, and L. C. Todd. 2004. An inter-site comparison of enamel hypoplasia in bison: implications for paleoecology and modeling Late Plains Archaic subsistence. Journal of Archaeological Science 31:1783–1794.
Osthoff, G., B. Beukes, A. C. Steyn, A. Hugo, F. Deacon, H. J. B. Butler, F. H. O'Neill, and J. P. Grobler. 2021. Milk composition of white rhinoceros over lactation and comparison with other Perissodactyla. Zoo Biology 40:417–428.
Owen-Smith, N. R. 1988. Megaherbivores: The Influence of Very Large Body Size on Ecology. Cambridge University Press, 392 pp.
Peigné, S., and P. J. Heizmann. 2003. The Amphicyonidae (Mammalia: Carnivora) from Ulm-Westtangente MN2, Early Miocene), Baden-Würteemberg, Germany: systematics and ecomorphology. Stuttgarter Beiträge Zur Naturkunde. Serie B, Geologie Und Paläontologie 343:1.
Peters, R. H. 1983. The Ecological Implications of Body Size. Cambridge University Press, 348 pp.
Raffi, I., B. S. Wade, H. Pälike, A. G. Beu, R. Cooper, M. P. Crundwell, W. Krijgsman, T. Moore, I. Raine, and R. Sardella. 2020. The Neogene period; pp. 1141–1215 in F. M. Gradstein, J. G. Ogg, M. Schmitz, and G. M. Ogg (eds.), Geologic time scale 2020. Elsevier.
Ripley, B., B. Venables, D. M. Bates, K. Hornik, A. Gebhardt, D. Firth, and M. B. Ripley. 2013. Package 'mass.' Cran r 538:113–120.
Risnes, S. 1998. Growth tracks in dental enamel. Journal of Human Evolution 35:331–350.
Rivals, F., A. Uzunidis, M. Sanz, and J. Daura. 2017. Faunal dietary response to the Heinrich Event 4 in southwestern Europe. Palaeogeography, Palaeoclimatology, Palaeoecology 473:123–130.
Schulz, E., J. M. Fahlke, G. Merceron, and T. M. Kaiser. 2007. Feeding ecology of the Chalicotheriidae (Mammalia, Perissodactyla, Ancylopoda). Results from dental micro-and mesowear analyses. Verhandlungen Des Naturwissenschaftlichen Vereins in Hamburg 43:5–31.
Scott, J. R. 2012. Dental microwear texture analysis of extant African Bovidae. Mammalia 76:157–174.
Scott, R. S., P. S. Ungar, T. S. Bergstrom, C. A. Brown, F. E. Grine, M. F. Teaford, and A. Walker. 2005. Dental microwear texture analysis shows within-species diet variability in fossil hominins. Nature

436:693–695.
Scott, R. S., P. S. Ungar, T. S. Bergstrom, C. A. Brown, B. E. Childs, M. F. Teaford, and A. Walker. 2006. Dental microwear texture analysis: technical considerations. Journal of Human Evolution 51:339–349.
Semprebon, G. M., P. J. Sise, and M. C. Coombs. 2011. Potential bark and fruit browsing as revealed by stereomicrowear analysis of the peculiar clawed herbivores known as chalicotheres (Perissodactyla, Chalicotherioidea). Journal of Mammalian Evolution 18:33–55.
Skinner, M. F., and J. D. Pruetz. 2012. Reconstruction of periodicity of repetitive linear enamel hypoplasia from perikymata counts on imbricational enamel among dry-adapted chimpanzees (*Pan troglodytes verus*) from Fongoli, Senegal. American Journal of Physical Anthropology 149:468–482.
Small, B. W., and J. J. Murray. 1978. Enamel opacities: prevalence, classifications and aetiological considerations. Journal of Dentistry 6:33–42.
Stefaniak, K., R. Stachowicz-Rybka, R. K. Borówka, A. Hrynowiecka, A. Sobczyk, M. M. Hoyo, A. Kotowski, D. Nowakowski, M. T. Krajcarz, E. M. E. Billia, D. Persico, E. M. Burkanova, S. V. Leschinskiy, E. van Asperen, U. Ratajczak, A. V. Shpansky, M. Lempart, B. Wach, M. Niska, J. van der Made, K. Stachowicz, J. Lenarczyk, J. Piątek, and O. Kovalchuk. 2020. Browsers, grazers or mix-feeders? Study of the diet of extinct Pleistocene Eurasian forest rhinoceros *Stephanorhinus kirchbergensis* (Jäger, 1839) and woolly rhinoceros *Coelodonta antiquitatis* (Blumenbach, 1799). Quaternary International 605–606:192–212.
Steininger, F. F. 1999. Chronostratigraphy, geochronology and biochronology of the Miocene" European Land Mammal Mega-Zones"(ELMMZ) and the Miocene" Mammal-Zones (MN-Zones)"; pp. 9–24 in G. E. Rössner and K. Heissig (eds.), The Miocene: Land Mammals of Europe. Verlag Dr. Friedrich Pfeil, München, Germany.
Steuer, P., K.-H. Südekum, T. Tütken, D. W. H. Müller, J. Kaandorp, M. Bucher, M. Clauss, and J. Hummel. 2014. Does body mass convey a digestive advantage for large herbivores? Functional Ecology 28:1127–1134.
Strömberg, C. A. 2011. Evolution of grasses and grassland ecosystems. Annual Review of Earth and Planetary Sciences 39:517–544.
Tafforeau, P., I. Bentaleb, J.-J. Jaeger, and C. Martin. 2007. Nature of laminations and mineralization in rhinoceros enamel using histology and X-ray synchrotron microtomography: Potential implications for palaeoenvironmental isotopic studies. Palaeogeography, Palaeoclimatology, Palaeoecology 246:206–227.
Taylor, L. A., T. M. Kaiser, C. Schwitzer, D. W. H. Müller, D. Codron, M. Clauss, and E. Schulz. 2013. Detecting Inter-Cusp and Inter-Tooth Wear Patterns in Rhinocerotids. PLOS ONE 8:e80921.
Tejada-Lara, J. V., B. J. MacFadden, L. Bermudez, G. Rojas, R. Salas-Gismondi, and J. J. Flynn. 2018. Body mass predicts isotope enrichment in herbivorous mammals. Proceedings of the Royal Society B: Biological Sciences 285:20181020.
Tissier, J., P.-O. Antoine, and D. Becker. 2020. New material of *Epiaceratherium* and a new species of *Mesaceratherium* clear up the phylogeny of early Rhinocerotidae (Perissodactyla). Royal Society Open Science 7:200633.
Tütken, T., T. W. Vennemann, H. Janz, and E. P. J. Heizmann. 2006. Palaeoenvironment and palaeoclimate of the Middle Miocene lake in the Steinheim basin, SW Germany: A reconstruction from C, O, and Sr isotopes of fossil remains. Palaeogeography, Palaeoclimatology, Palaeoecology 241:457–491.
Upex, B., and K. Dobney. 2012. Dental enamel hypoplasia as indicators of seasonal environmental and physiological impacts in modern sheep populations: a model for interpreting the zooarchaeological record. Journal of Zoology 287:259–268.
Wasserstein, R. L., and N. A. Lazar. 2016. The ASA Statement on p-Values: Context, Process, and Purpose. The American Statistician 70:129–133.
Werner, J. 1994. Beiträge zur Biostratigraphie der Unteren Süßwasser-Molasse Süddeutschlands: Rodentia und Lagomorpha (Mammalia) aus den Fundstellen der Ulmer Gegend. Stuttgarter Beiträge Zur Naturkunde Serie B 200:1–263.
Westerhold, T., N. Marwan, A. J. Drury, D. Liebrand, C. Agnini, E. Anagnostou, J. S. K. Barnet, S. M. Bohaty, D. D. Vleeschouwer, F. Florindo, T. Frederichs, D. A. Hodell, A. E. Holbourn, D. Kroon, V. Lauretano, K. Littler, L. J. Lourens, M. Lyle, H. Pälike, U. Röhl, J. Tian, R. H. Wilkens, P. A. Wilson, and J. C. Zachos. 2020. An astronomically dated record of Earth's climate and its predictability over the last 66 million years. Science 369:1383–1387.
Wickham, H. 2016. Ggplot2: Elegant Graphics for Data Analysis. Springer-Verlag, New York, 260 pp.

Wickham, H., and L. Henry. 2020. Tidyr: Tidy messy data. R Package Version 1:397.
Wilke, C. O. 2020. cowplot: Streamlined Plot Theme and Plot Annotations for “ggplot2”. R Package Version 1.1.0.
Zachos, J. C., N. J. Shackleton, J. S. Revenaugh, H. Pälike, and B. P. Flower. 2001. Climate Response to Orbital Forcing Across the Oligocene-Miocene Boundary. Science 292:274–278.
Zanazzi, A., A. Fletcher, C. Peretto, and U. Thun Hohenstein. 2022. Middle Pleistocene paleoclimate and paleoenvironment of central Italy and their relationship with hominin migrations and evolution. Quaternary International 619:12–29.
Zecchini, A. 1998. Le Rhinocéros: Au Nom de La Corne. Editions L’Harmattan, 272 pp.
Ziegler, R. 1989. Heterosoricidae und Soricidae (Insectivora, Mammalia) aus dem Oberoligozan und Untermiozan Suddeutschlands. Stuttgarter Beitrage Zur Naturkunde Serie B 154:1–73.
Ziegler, R. 1990a. Didelphidae, Erinaceidae, Metacodontidae und Dimylidae (Mammalia) aus dem Oberoligozän und Untermiozän Süddeutschlands: Stuttgarter Beiträge zur Naturkunde: Reihe B (Geologie und: Paläontologie). Stuttgarter Beiträge Zur Naturkunde Serie B 158:1–99.
Ziegler, R. 1990b. Talpidae (Insectivora, Mammalia) aus dem Oberoligozän und Untermiozän Süddeutschlands. Stuttgarter Beiträge Zur Naturkunde Serie B 167:1–59.